

CONTRIBUTIONS TO OUR KNOWLEDGE OF AMERICAN CARBONIFEROUS FLORAS¹

V. HETERANGIUM

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Our knowledge of Pteridosperm stem remains referred to the genus *Heterangium* is based chiefly on the earlier works of Williamson and Renault and the later detailed studies of Scott and Hirmer. Judging from its rather frequent occurrence in England, Scotland and on the Continent, the genus was well established throughout the greater part of the Carboniferous period.

Of the various plant organs that are assigned with some degree of certainty to the Pteridospermeae, *Heterangium* is of special significance because of its comparatively primitive structure as well as its occurrence in the early Calciferous Sandstone Series. It seems very likely that when its reproductive organs become better known we shall have a much clearer concept of how this early group of seed plants originated. An exhaustive review of the genus is unnecessary here inasmuch as the better-known species are adequately treated in certain of the standard texts and more detailed accounts may be found in the contributions of Scott ('17) and of Hirmer ('33). The latter work contains a useful key which outlines the major variations within the genus.

Although it has been known for some few years that *Heterangium* occurs in American Pennsylvanian coal-balls, no descriptions have been published. In 1935 Graham listed *H. tiliaeoides* as present in coal-balls from the McLeansboro horizon in Illinois, but his only comment relative to its occurrence was that, "Several stems were identified." In 1938 Fisher and Noé also reported *Heterangium* species from Calhoun coal-balls, but there were no accompanying descriptions. They also listed *H. Grievii* as having been found, which is rather surprising in view of its much earlier occurrence in the Calciferous Sandstone Series in Scotland. These brief references constitute, so far as I am aware, the only published accounts of the occurrence of the genus in America.

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***Heterangium americanum*, sp. nov.—**

The following description is based on a number of stem and petiole remains found in coal-balls from the Calhoun coal, Richland County, Illinois. The locality is in the upper part of the McLeansboro formation and is of upper Pennsylvanian age. A single specimen of *Heterangium* has been collected by the author from the Herrin (No. 6) coal at the Pyramid Mine three miles south of Pinckneyville, Illinois. This constitutes the top of the Carbondale formation, and although it lies somewhat below the Calhoun coal (Schopf, '41, chart p. 9) this particular specimen is referable to *H. americanum*.

The specimens from Richland County consist of stem fragments bearing petioles, as well as isolated remains of both, and although the size and comparative development of secondary wood vary somewhat there are no distinctive features that necessitate segregation of the specimens into more than one species.

***Primary Wood.*—**

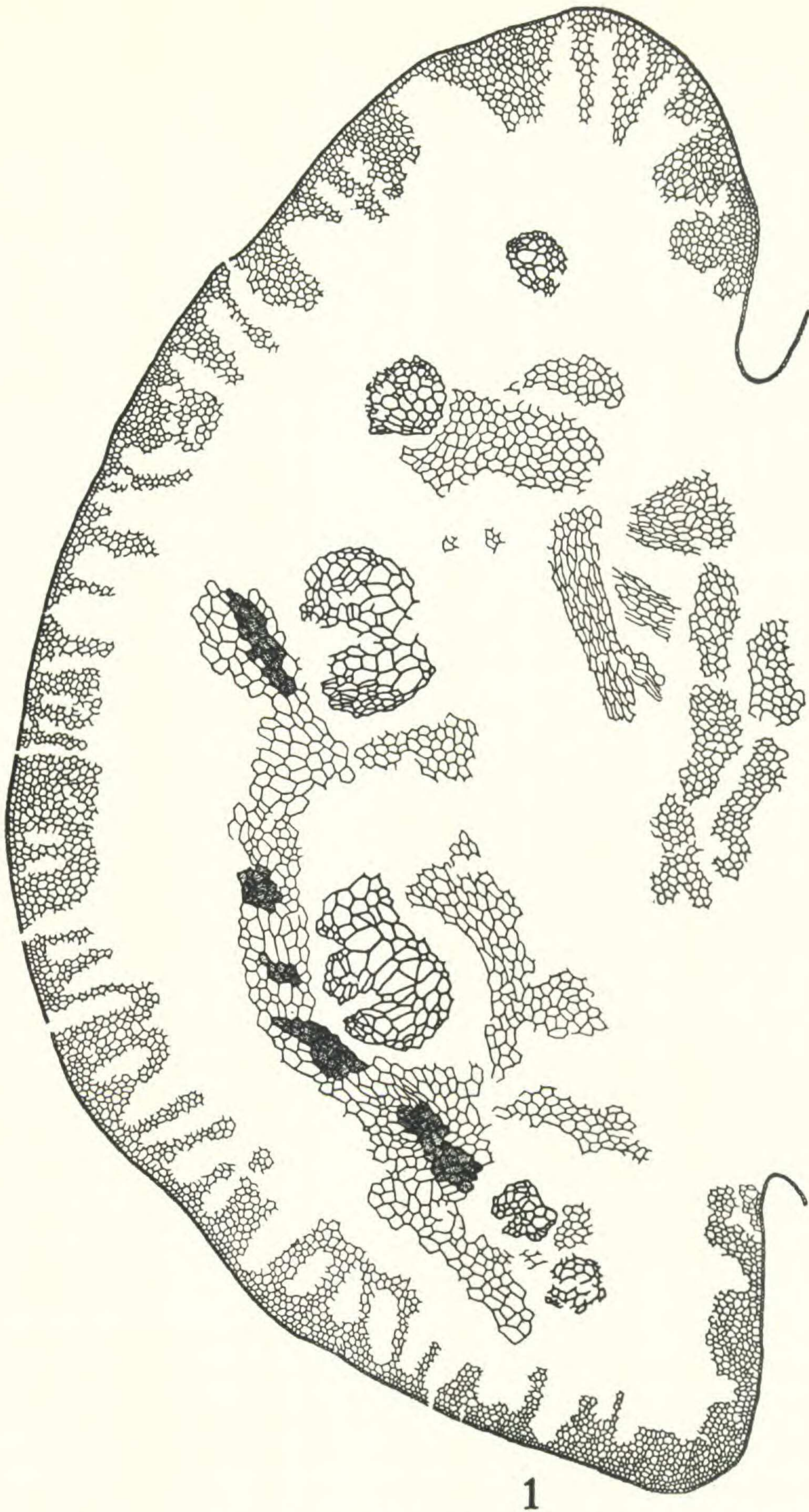
The diameter of the primary xylem varies in different specimens from 1.75 mm. to 4 mm. As in the European species of *Heterangium*, the protoxylem groups occupy a position very close to the periphery. Where it is possible to distinguish the protoxylem with certainty a few primary tracheids can be observed external to it although these pass almost imperceptibly into the secondary xylem. The protoxylem thus occupies an excentrically mesarch position though it is very close to being exarch.

The large metaxylem cells (pl. 25, fig. 3), which average about 260 μ in diameter, are uniformly distributed throughout the parenchyma of the central cylinder. They may occur singly or in small groups of 2, 3 or 4 cells, but usually not more than that number except in the peripheral region where they pass into the protoxylem. The tracheids of the latter may be as small as 15 μ in diameter, while the secondary tracheids average about 65 μ .

The pitting of the primary tracheids differs in no way from that described for other species.

***Secondary Wood.*—**

Some of the stems exhibit no secondary growth at all, while others show as much as 5 mm. (figs. 1, 4). The wood rays vary greatly both in height and breadth as well as in the size of the component cells. Text-fig. 2, drawn with the aid of a camera-lucida, shows a representative tangential section. The rays may consist of but a



Text-fig. 1. *Heterangium americanum*: A drawing prepared with the aid of a camera lucida showing division of the lateral and lobing of the central trace branches in a petiole. CB386.C.T11, $\times 17.5$.

single row of cells while others are uniseriate but attain a height of 3 mm. or more. One such slender ray may be observed near the right-hand side extending the entire height of the figure. Elongate fusiform bi- or triseriate rays are common and may even reach a width of 6 or 7 cells although all of these broad rays that were observed were undergoing division.

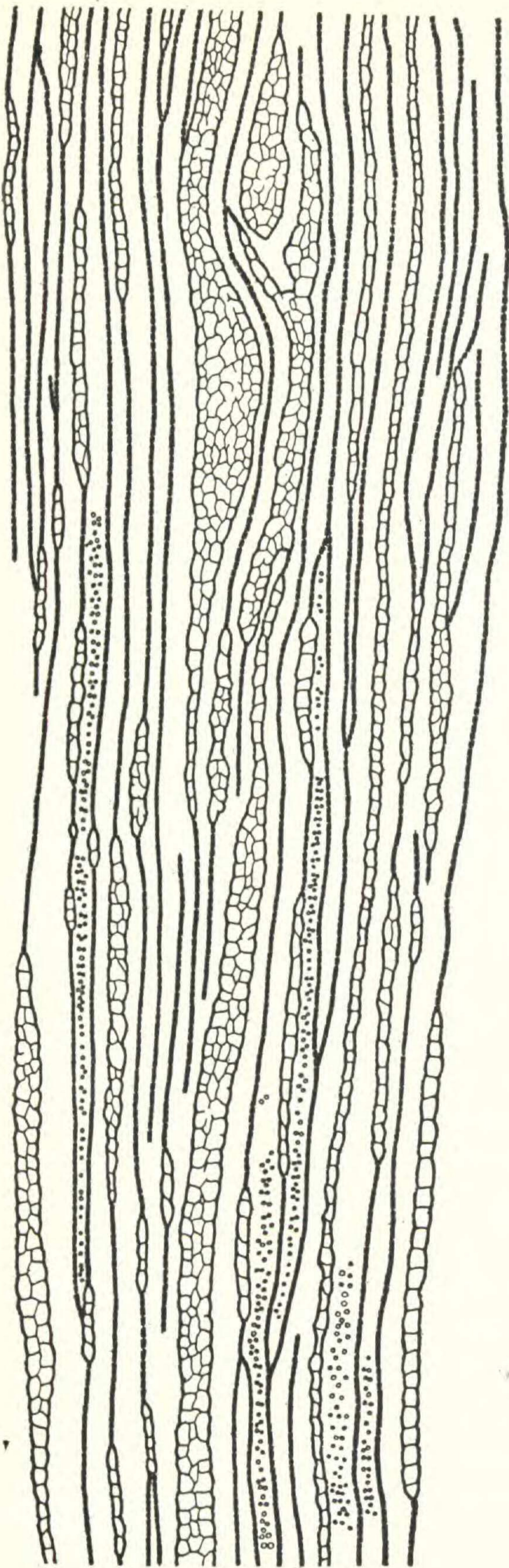
The radial walls of the tracheids are characterized by closely compacted angular pits (text-fig. 4) like those found in other species of *Heterangium*, as well as certain other probably closely related Pteridosperms such as *Lyginopteris*, *Rhetinangium* and *Stenomyelon*. The pit borders are not well preserved in the radial walls, but where they can be observed the orifice appears to be rather broadly oval-shaped and horizontally elongated.

The pits in the tangential walls are quite distinct from those in the radial walls, being nearly circular and loosely arranged in 1, 2 or 3 rows (text-fig. 3). The narrow orifice extends almost the entire diameter of the pit, and forms a cross with the pit in the wall of the adjacent tracheid.

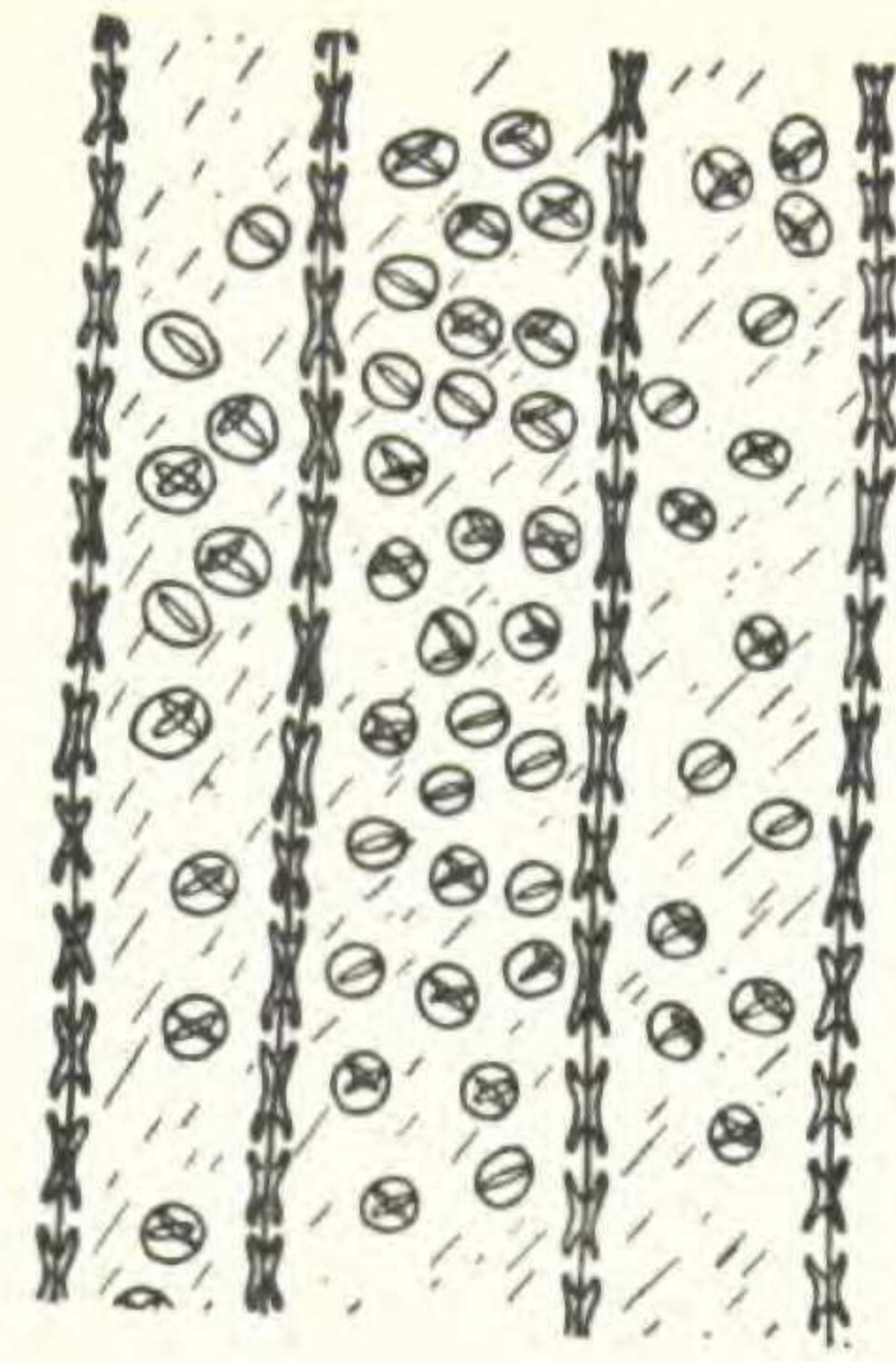
Leaf Trace and Petiole.—

Owing to the fact that all the stems and petioles are short fragments, it has not been possible to follow any individual leaf trace from its origin in the stele out into the petiole. However, a sufficient number of specimens showed various stages in the course of the trace to give a reasonably complete picture of its anatomy.

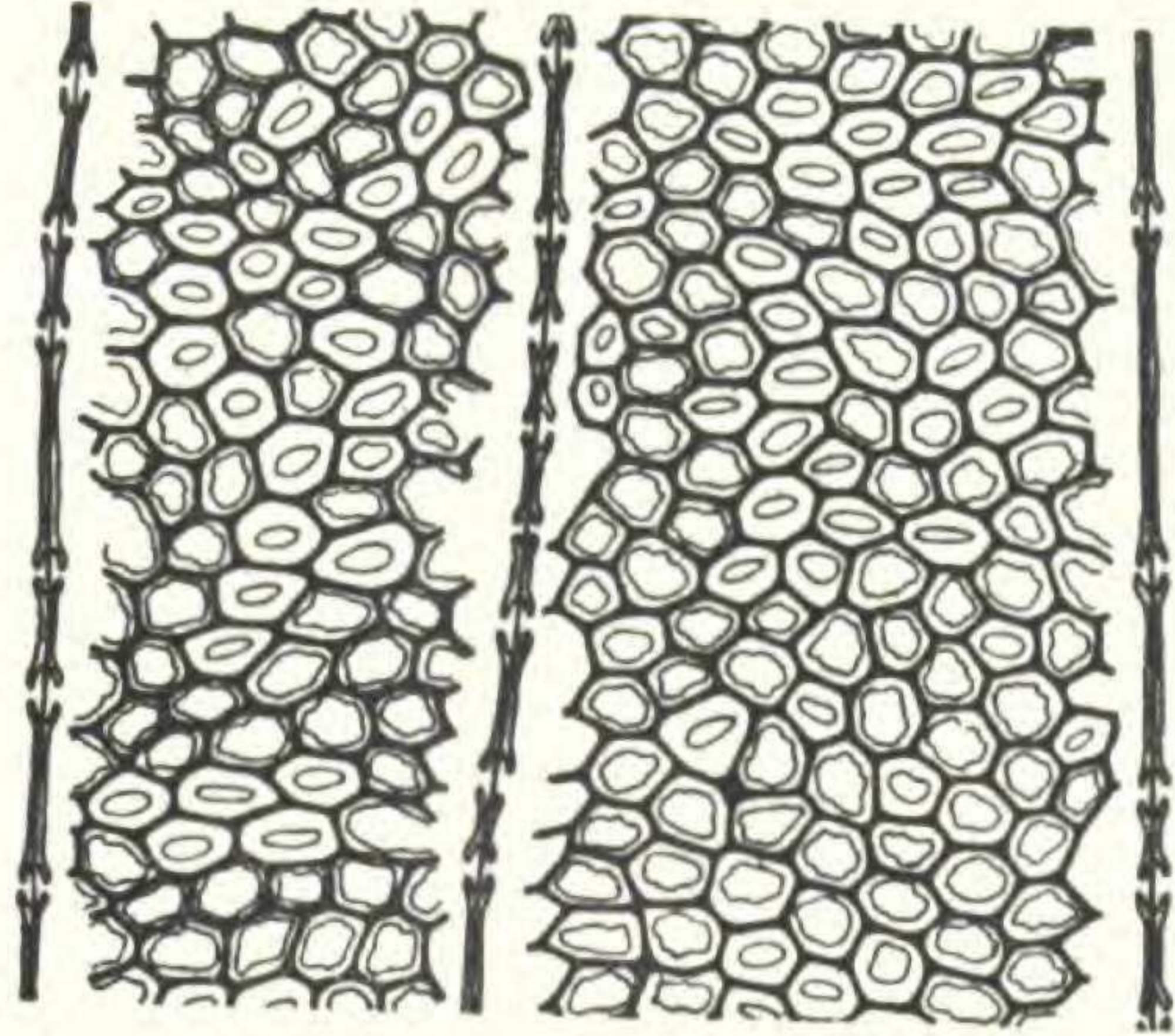
The leaf trace originates from the periphery of the primary xylem as two distinct bundles about two mm. apart (text-fig. 5). They start to divide almost immediately and are two-lobed at the time of their departure from the stele. In their passage through the cortex the division is completed and four separate bundles enter the base of the petiole (fig. 2). The outer or lateral branches (fig. 2, L₁, L₂) resulting from the first division then divide into two small bundles which pass out toward the wing of the petiole (fig. 5, L_{1a}, L_{1b}; text-fig. 1). The two central bundles (fig. 2, c₁, c₂) resulting from the first division then start to divide into three bundles each (fig. 5; text-fig. 1). That this division began prior to the separation of the petiole from the stem is evidenced in text-fig. 1 which represents a petiole still connected to its stem. One of the large central bundles is clearly three-lobed while the other has not quite reached this stage. Another petiole found isolated (fig. 5) exhibits the three-lobed condition in both bundles. No specimens have been



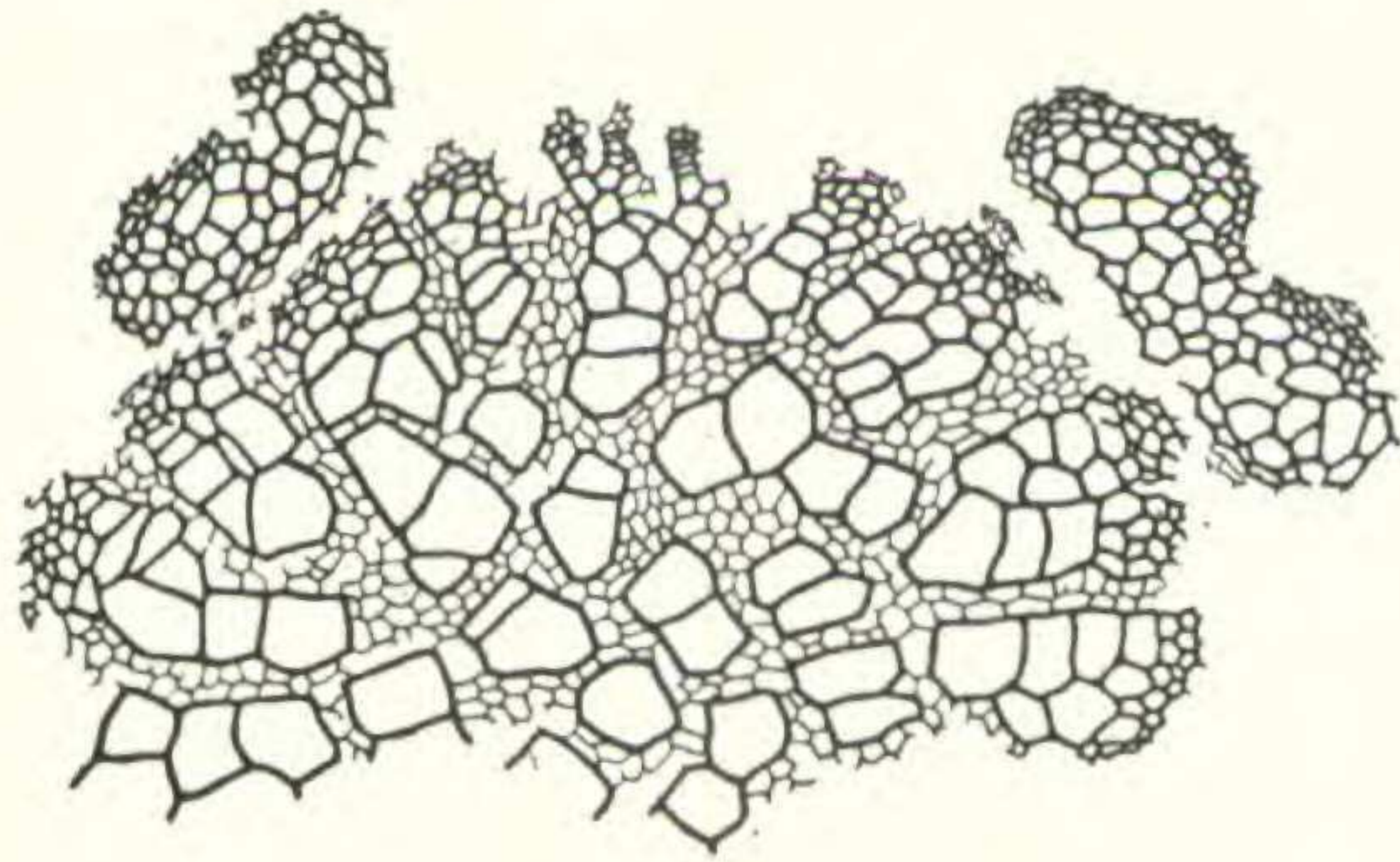
2



3



4



5

Text-figs. 2-5. *Heterangium americanum*: fig. 2, tangential section through the secondary wood. CB542.B1.F48, $\times 62$; fig. 3, pitting in the tangential walls of the secondary tracheids. CB542.B1.F48, $\times 265$; fig. 4, pitting in the radial walls of the secondary tracheids. CB542.B1.F48, $\times 265$; fig. 5, portion of a stele in transverse section showing the two traces that will enter a petiole. CB386.D2.T10, $\times 17.5$.

found showing a higher level of the petiole than that illustrated in this figure. It seems very likely, however, that the two central strands soon divided, resulting in a total of ten at a slightly higher level. No evidence is available pertaining to the further division of the traces or the petiole as a whole.

Outside the bundles of the petiole shown in text-fig. 1 there may be noted a series of sclerotic nests embedded in large, thin-walled parenchymatous cells. The outer cortex is not well preserved, but judging from the more or less regular sequence of cavities (text-fig. 1) it seems likely that this zone consisted of alternate bands of fibrous and parenchymatous cells, the latter having decayed.

The extra-stelar tissues of the stems are not well preserved although specimen CB542 displayed the horizontal sclerotic plates characteristic of the outer cortex of the genus.

Diagnosis.—

Primary xylem from 1.75 to 4. mm. in diameter, metaxylem tracheids about 260 μ in diameter and uniformly distributed singly or in groups of 2, 3 or 4 cells; secondary wood well developed in some specimens, tracheids pitted on radial and tangential walls, rays variable in vertical and tangential dimensions; leaf trace double from the time of its origin, each trace dividing in its course through the cortex; of the four bundles entering the petiole the two central ones become three-lobed while the two marginal ones each divide to form two distinct bundles.

Locality and horizon: Richland County, Illinois; Calhoun coal, McLeansboro formation, upper Pennsylvanian and Herrin coal, Pyramid Mine, Perry County, Illinois; upper Carbondale formation.

All figured preparations are preserved in the Washington University collections, St. Louis. The original blocks and a representative set of preparations are deposited with the Illinois State Geological Survey.

Discussion.—

In his consideration of the British Coal-Measure Heterangium Scott ('17) proposed the sub-genera *Eu-heterangium* and *Polyangium* to include those species characterized by having the vascular system of the petiole originate as a single or double bundle respectively. Hirmer ('33) recognizes six species in the *Polyangium* group, in which *H. americanum* belongs. The two German species,

H. Kukuki and *H. Hoppsteadteri*, differ rather strikingly from the Illinois *Heterangium* in the arrangement of the metaxylem tracheids. In the last they usually occur in 2- or 3-celled groups which are uniformly distributed. The contrast is especially true in *H. Kukuki*, where the tracheid cells are in large groups of 10 or more and the groups are separated by prominent parenchymatous "rays" (cf. Hirmer, '33, pl. 8, fig. 2).

The affinities of the Illinois species seem to lie close to the English *H. tiliaeoides* and *H. shoreense*. Graham recognized this relationship when he assigned his specimen to the former. The small size of the metaxylem tracheid groups in *H. americanum* offers a character which likewise sets it apart from these English *Heterangium*s and which I believe is worthy in itself of specific distinction. Another feature, however, that has not been described for the other species is the apparent tri-partite branching of the central traces in the petiole (fig. 5). It may be, of course, that comparable portions of the petiole are present among the English specimens but until such is shown to be the case this may be considered as characteristic of *H. americanum*. In view of these differences it seems advisable to assign this new specific name to our specimens.

Acknowledgement.—

I wish to express my appreciation to the Illinois State Geological Survey, and especially to Dr. James M. Schopf of that organization, for the opportunity of studying and describing these American specimens of *Heterangium*.

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EXPLANATION OF PLATE

PLATE 25

Heterangium americanum

Fig. 1. Slightly oblique transverse section showing well-developed secondary wood. CB542.A1.S13, $\times 8.5$.

Fig. 2. Transverse section of a portion of a stem and attached petiole. CB386.D.T21; L_1, c_1 and L_2, c_2 are the branch traces resulting respectively from the two traces entering the petiole, $\times 8.5$.

Fig. 3. Stele of same, $\times 12$.

Fig. 4. A smaller stem showing secondary wood. CB323.A2.S9, $\times 8.5$.

Fig. 5. An isolated petiole showing partial division of the central trace branches. CB323.A2.S9, $\times 8.5$.

Photographs by Eloise Pannell.